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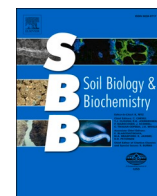
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Species richness and functional diversity of isopod communities vary across an urbanisation gradient, but the direction and strength depend on soil type

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ABSTRACT

Urbanisation involves major changes in environmental conditions such as light, temperature, humidity and noise levels, but the effect of urbanisation on soil conditions and soil biodiversity has received less attention. The reported effects on species richness across a rural to urban landscapes are not unequivocal. Positive, negative and neutral effects have been found, but what is causing this ambiguity in the relationship between species richness and urbanisation is poorly understood. Here we tested whether and how urbanisation affects isopod diversity and whether this depends on habitat soil type. We recorded isopod species presence and soil type in each 1 km² grid cell in a 500 km² area in and around the city of Amsterdam, the Netherlands. We analysed the relationship between the number of species and the most important traits (body size and drought- and inundation resistance), the percentage built-up area, and soil type (peat or clay) across a rural-urban landscape gradient. Because many studies find a negative effect of urbanization on biodiversity, we expected a decrease in isopod species richness by increasing amount of built-up area. We found a negative association between isopod species richness and the amount of built-up area across the rural-urban landscape gradient when rural soils contained clay, while for rural soils containing peat the highest species richness was found at intermediate levels of urbanisation. Hence, the relationship between isopod species richness and the level of urbanisation was mediated by soil type. We also found a significant relationship between percentage built-up area and functional traits, irrespective of soil type. Specifically, the percentage built-up area showed a positive correlation with isopod drought resistance as well as body size. These results together demonstrate (1) that soil type variation introduces an important, but often overlooked context-dependency in the effect of urbanisation on biodiversity and (2) that a functional trait approach is an important tool for understanding general effects of environmental change on biodiversity, irrespective of context-dependency.

1. Introduction

Urbanisation is seen as a major cause of habitat and biodiversity loss worldwide (McKinney, 2002; Seto et al., 2012). The transformation from natural to urban ecosystems results in fragmentation of the natural environment, with smaller habitat fragments of altered quality, modification of local climate, and, hence, an increase in habitat patch isolation (Goddard et al., 2010). Understanding the interactive effects of these factors on the occurrence of species and the composition of natural communities, and how these altered communities in turn affect the ecosystem, is a pressing point on the research agenda for better predictions on ecosystem functioning under global changes (Díaz et al.,

2013).

Urban development has been shown to reduce species richness and evenness in habitat patches for many taxonomic groups (Grimm et al., 2008), and can even lead to complete community replacement. Although most studies show a negative effect of urbanisation on species richness, some studies have found a neutral effect (e.g. Pavao-Zuckerman and Coleman, 2007; Vilisics et al., 2007; Baiser and Lockwood, 2011) or even a positive effect of a low level of urban development on biodiversity (Vilisics et al. (2009), Ramirez et al., (2014), Caruso et al. (2017)). These patterns, which also depend on which substrates are actually sampled (e.g. soil versus non-soil) lead to an overall hump-shaped relationship (McKinney, 2008). The influence of

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urbanisation on biodiversity can thus be positive, neutral or negative, suggesting that land-use change alone does not explain species richness or diversity. Urbanisation effects might depend on, for instance, the environmental conditions in the original natural environment, the community composition of organisms in it, the potential of the non-urban communities outside the city to be a source for colonising green “islands” in the city, how green spaces are structured, positioned and maintained within the city and how connected they are to each other, and on the type and intensity of urbanisation (Jesse et al., 2018). Here, we will study the effect of urbanization on soil biodiversity and the possible mediating effect of environmental factor of soil type.

Soil fauna, such as litter fragmenters like isopods, millipedes and earthworms, but also nematodes and microarthropods, play important roles in ecosystem processes (Lavelle, 1997; Hättenschwiler et al., 2005; Bardgett and Van Der Putten, 2014), and how urbanisation affects their species composition, and hence soil functioning, is a pressing question. Most urbanization studies have focused on above ground, species, biodiversity and processes (e.g. pollination). In comparison, relatively few studies have focused on changes in soil conditions and diversity have been carried out (but see Ramirez et al., 2014; Bogyó et al., 2015; Caruso et al., 2017). However, urbanization can strongly alter soil conditions (e.g. texture, soil moisture levels, nutrient content). Both disturbance and management (i.e. soil improvement, irrigation) can change the soil environment (Pouyat et al., 2010). Cities are warmer and drier than their rural surroundings (“urban heat islands”; Dale and Frank, 2014), as buildings store heat during the day and radiate energy during the night (Roth et al., 1989; Oke et al., 1991), and urban evaporation is enhanced due to these higher temperatures (Pickett et al., 2011). Also, water infiltration and water storage are reduced because of pavement or compaction of the soil surface (Jacobson, 2011; Yang and Zhang, 2015), adding to the often lower soil water content in comparison to surrounding rural landscapes in summer. A large part of this run-off water in the inner city (high level of urbanization) quickly disappears from the ecosystem via the rain water drainage system. Remaining water has a difficulty to infiltrate in green patches due to soil compaction. This results in reduced storage of water and soil drought during the summer and negatively affects isopods sensitive to drought (as our trait data also suggests). Moreover, literature shows that cool temperature, dense vegetation cover (i.e. parks) and high surface moisture conditions coincide, as well as high temperature, sparse vegetation cover (i.e. flower beds in inner city) and low soil surface moisture conditions (see among others Jiang et al., 2015). An often opted explanation for the heat island effect under high levels of urbanization is low soil moisture, which results in a reduction in evapotranspiration leading to high temperatures compared to areas that store more water (Pickett et al., 2011). This rise in temperature can increase the loss of the already low amounts of soil water even further, adding to soil drought. Urban habitat conditions might therefore act as a strong environmental filter (Aronson et al., 2016) and select for different functional traits of species than rural habitats, in particular for tolerance and resistance traits (e.g. drought or flooding tolerance).

Isopods are known to be very sensitive to changes in soil moisture content, which can invoke significant shifts in species abundance, species richness and vertical stratification across soil moisture gradients (Morón-Ríos et al., 2010; Blankinship et al., 2011; Dias et al., 2013; Fournier et al., 2015). Soil types differ in pore volume, soil moisture content and dynamics, nutrient availability and pH (Bardgett, 2005; Lavelle and Spain, 2001). Clay soil has a high water holding capacity, resulting in a good buffer for strong soil moisture fluctuations (Hillel, 2013). Also, clay soil has a high bulk density, which may act as a physical barrier to water infiltration. In peat soils on the contrary, bulk density is low due to a high organic matter content and average pore size is large compared to that in clay, resulting in a higher water content. However, peat soils dry out faster than clay soils. The calcium content of peat soil is much lower than that of marine clay and, as a consequence, soil pH values are relatively low (Bolt and Bruggenwert, 1978).

Terrestrial isopods need to take up calcium from their environment for their exoskeleton (Hornung, 2011), which partly may explain the low isopod species diversity in peat as compared to clay soils. In this way, soil type may exert strong selection pressures for species with traits reflecting different resource needs and tolerances to environmental conditions. The degree of drought and inundation resistance varies greatly among isopod species (Dias et al., 2013) and help us to understand changes in species distributions across an urban gradient. As isopods are macrodetritivores that enhance litter decomposition and nutrient mineralization, changes in their (functional) diversity may impact carbon and nutrient turnover of soil organic matter, C sequestration and soil fertility (Heemsbergen et al., 2004; Lavorel et al., 2013; Bílá et al., 2014; David, 2014; Filser and Jiménez, 2016).

Variation in functional traits is often more strongly related to environmental change than taxonomic composition (Bokhorst et al., 2012) and can be used to predict community shifts over an environmental gradient or following environmental change (Violle et al., 2007; Dias et al., 2013). Here, we analysed differences in the effect of urbanisation on isopod species richness and functional diversity for different soil types. We expect that intermediate levels of urbanisation have a positive effect on isopod biodiversity, while a further increase in the level of built-up area will have a negative effect (McKinney, 2008). This will result in a unimodal relationship between percentage of built-up area and number of species. However, in rural soils that have a very high species richness, like clay soils with a high pH and rich in calcium are preferred habitat for many isopod species (Harding and Sutton, 1985; Berg et al., 2008), even moderate levels of urbanisation will have a negative effect on species number. Second, we predicted an increase in average drought resistance and a decrease in average inundation resistance of the isopod communities along a gradient from rural to urban habitat for both soil types. The combination of higher temperatures as a result of urban heating and an increase in impervious surface area contributes to lower soil moisture in cities compared to rural areas (Dale and Frank, 2014), which should benefit drought tolerant species and deter drought sensitive species. Third, we expected an increase in the average body size of isopods from rural to urban landscapes, because the two above-mentioned ecophysiological traits are related to body size (Dias et al., 2013). Finally, we tested the effect of the type of green (urban green *versus* rural green) on species richness. We tested our hypotheses in the city of Amsterdam, the Netherlands, and its surrounding landscape. Here, clear gradients of rural to urban landscapes exist, on contrasting clay and lowland peat soils. In this area we surveyed the existing isopod communities, and estimated soil type, the percentage of built-up area and rural and urban habitat area in square km grid cells.

2. Materials and methods

2.1. Study area

The study was conducted in and around the city of Amsterdam (52°22.4418' N, 4°53.3814' E), the Netherlands. The city originally developed on peat soil in the north-east of the study area and on clay soil in the south-west, while more recently sand has been deposited on top of both soil types in large parts of the study area to stabilize the soil for new development (Fig. 1). It presents an ideal area to study the interaction between soil type and level of urbanisation on terrestrial isopod biodiversity and trait composition.

The study area was divided into 432 square grid cells (18 by 24 grid cells) of 1 km² each (Fig. 1) following the Dutch grid or RD system. Data on the level of urbanisation in 1996 was subtracted from a land-use map of Amsterdam (Fig. 1a, CBS, 1996). For each grid cell, we calculated the proportion built-up area and habitat area (of the total land surface area) using ArcGIS for Desktop (10.4.1). Habitat area was subdivided into natural habitat (e.g. semi-natural grasslands, and agricultural fields with broad semi-natural margins and ditches) and urban habitat (any vegetated space related to urbanisation, e.g. parks, sport fields, allotments,

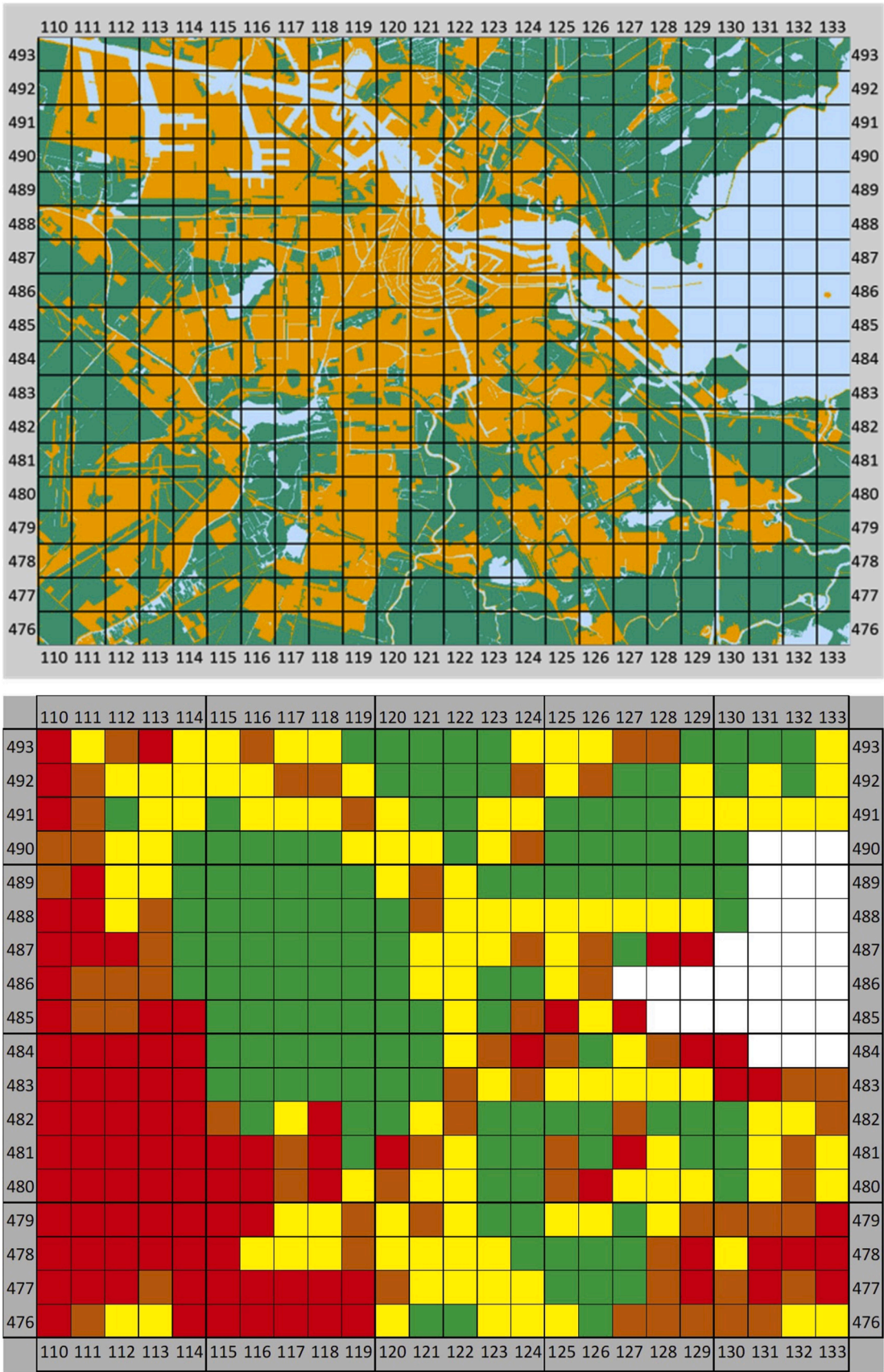


Fig. 1. Map of the city of Amsterdam and surrounding area with a grid with grid cells of 1 by 1 km as an overlay. Upper panel gives an overview of built-up (orange) and green areas. Lower panel gives the soil type per grid cell within the city of Amsterdam. Green >90% peat, yellow = 50–90% peat, orange = 50–90% clay with peat and red >90% clay. White grid cells contain only water. Numbers on the side of the tables indicate coordinates of the Dutch grid system. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

gardens). Built-up area was defined according to coverage by buildings, roads, squares or other hard man-made substrates.

Information on soil type was extracted from a soil type map (De Gans, 2006). Two basic soil types were present in the study area: peat and clay soils. According to the WRB classification scheme, these soils can be categorised as Histosol and Fluvisol, respectively. Sand was not used as a separate soil type, because it was only found under roads and buildings. Below any recent buildings or major development projects a deep layer of sand has been supplied on top of one of the two original soil types before construction (personal comm. municipality of Amsterdam), but these layers are not accessible for isopods. Grid cells were divided into four soil type categories along a gradient from pure clay to pure peat soils: clay soil (>90% clay), peat soil (>90% peat), peat with clay soil (50–90% peat) and clay with peat soil (50–90% clay). Parks are usually located on previously natural soils (often remnants of rural habitat space). In total we investigated 352 of the 432 grid cells, of which 121 contained peat soil, 74 had clay soil, 93 clay with peat and 64 had peat with clay (Fig. 1b). The level of urbanisation for all soil types ranged between 0 and 100% built-up area per grid cell (Fig. S3) and the proportions of built-up area were evenly distributed over the four soil type categories (Fig. S4). Grid cells (80 in total) that were covered for more than 90% with water or that contained more than 10% habitat cover that was inaccessible to survey isopods, i.e. private properties, restricted areas or rural sites without roads, were excluded from analyses.

2.2. Species survey

Data on presence or absence of terrestrial isopods were based on an extensive terrestrial isopod survey conducted between 1996 and 1998 with the aim to construct distribution maps for several species for the Amsterdam region (Berg et al., 1998). Each grid cell was visited once by on average three well-trained soil ecologists for approximately 1 h, during which time the major habitats and soil types were surveyed and isopod species presence were noted. The typical microhabitats that were

sampled by hand, using a hand-rake, were stones, standing and lying dead wood, branches, leaf litter, garbage, and root mats against walls or concrete constructions. The actual area sampled within this hour differed between grid cells but not soil types, depending on site heterogeneity in major habitats. The aim of the survey was to collect as many as possible of all species present in each grid cell.

Each species was identified to the species level. Nomenclature follows Schmalfuss (2003). *Trichoniscus pusillus* and *T. provisorius* are difficult to separate morphologically. Only males can be used to identify the species with certainty, which is made problematic as *T. pusillus* is largely parthenogenetic (at most 1–3% males in population (Fussey, 1984). Recent surveys in the Netherlands, followed by identification specimens using the genetical marker CO1 have revealed that *T. provisorius* is only found in rich soils, among others in the Amsterdam region (personal observation last author) and that they are always mixed with *T. pusillus*. Pure *T. provisorius* populations have so far not been found in the Netherlands, while pure *T. pusillus* populations have been observed in poor soils, such as on sand and peat. We therefore aggregated the two species under the name *T. pusillus* s.l.

2.3. Standardized trait measurements

For the observed isopod species, three traits were selected that relate to soil hydrology, i.e. body size, drought tolerance and inundation tolerance (Dias et al., 2013), all measured under standardized conditions (following Moretti et al., 2017). Trait data was derived from Dias et al. (2013) and data of missing species was complemented with own measurements. Isopods (Table 1) were collected by hand sampling in the Netherlands (see Dias et al. (2013) for the exact locations per species). Animals were kept in plastic pots ($\varnothing = 13$ cm; $H = 6$ cm) with a 2 cm thick bottom of moist plaster of Paris and a 1.5 cm thick layer of moist substrate from the collection site. The pots were stored in a climate room (15 °C, 75% RH, 16 h: 8 h light/dark) for a minimum of one week and a maximum of six weeks prior to trait measurements, in order to acclimate

Table 1

List of the observed isopod species, and corresponding value of three functional traits. Species are sorted from high to low occurrence (% grid cells in which species was found). Values are the mean \pm standard error of the mean based on 10 individuals per species.

Species	Family	Maximum body length (mm) ^a	Drought resistance (hours) ^b	Inundation resistance (hours) ^c	Occurrence (% of total number of grid cells)
<i>Porcellio scaber</i> Latreille, 1804	Porcellionidae	18	51.3 \pm 4.11	22.9 \pm 3.7	100
<i>Philoscia muscorum</i> (Scopoli, 1763)	Philosciidae	12	31.8 \pm 3.35	10.7 \pm 2.7	94.2
<i>Oniscus asellus</i> Linnaeus, 1758	Oniscidae	16	22.1 \pm 2.30	22.2 \pm 4.7	90.9
<i>Trichoniscus pusillus</i> s.l. Brandt, 1833	Trichoniscidae	5.0	2.38 \pm 0.19	192 \pm 34.5	90.6
<i>Armadillidium vulgare</i> (Latreille, 1804)	Armadillidiidae	18	73.6 \pm 5.85	46.7 \pm 2.6	77.9
<i>Trachelipus rathkii</i> (Brandt, 1833)	Trachelipodidae	15	22.6 \pm 2.18	255 \pm 46.7	43.2
<i>Trichoniscoides sarsi</i> Patience, 1908	Trichoniscidae	5.0	2.60 \pm 0.15	249 \pm 28.1	33.8
<i>Platyarthus hoffmannseggii</i> Brandt, 1833	Platyarthridae	4.0	3.64 \pm 0.31	290 \pm 60.8	30.2
<i>Ligidium hypnorum</i> (Cuvier, 1792)	Ligiidae	9.0	4.54 \pm 0.33	36.9 \pm 4.8	29.5
<i>Haplophthalmus danicus</i> Budde-Lund, 1880	Trichoniscidae	4.0	2.82 \pm 0.17	181 \pm 39.5	25.3
<i>Trichoniscoides albidus</i> (Budde-Lund, 1880)	Trichoniscidae	5.0	2.17 \pm 0.21	260 \pm 28.5	13.0
<i>Haplophthalmus mengii</i> (Zaddach, 1844)	Trichoniscidae	4.0	2.21 \pm 0.22*	333 \pm 31.1	11.4
<i>Trichoniscus pygmaeus</i> Sars, 1899	Trichoniscidae	2.5	2.41 \pm 0.18*	282 \pm 29.3	8.44
<i>Porcellio spinicornis</i> Say, 1818	Porcellionidae	12	83.5 \pm 8.19	28.2 \pm 4.9	5.84
<i>Metatrachoniscoides leydigii</i> (Weber, 1880)	Trichoniscidae	4.0	2.26 \pm 0.13	260 \pm 28.5	1.62
<i>Androniscus dentiger</i> Verhoeff, 1908	Trichoniscidae	6	5.52 \pm 0.17	3.7 \pm 19.2	1.30
<i>Porcellionides pruinosus</i> (Brandt, 1833)	Porcellionidae	12	18.6 \pm 1.97*	39.4 \pm 20	1.30
<i>Hyloniscus riparius</i> (Koch, 1838)	Trichoniscidae	6.5	3.09 \pm 0.32*	424 \pm 119.5	0.97

^a Data derived from Vandel (1960, 1962), Dahl and Peus (1966), Gruner (1966), Hopkin (1991) and Berg and Wijnhoven (1997). We took the highest reported body length.

^b Trait data derived from Dias et al. (2013) and from own measurements (with asterisk) following Moretti et al. (2017).

^c Based on own measurements.

the animals to experimental conditions (Dias et al., 2013).

To standardize the condition of species at the start of the measurements, we kept each individual without food in small plastic vials (\varnothing 2.0 cm, H = 3.0 cm, 9.4 cm³) with a layer of moist plaster of Paris and mesh on top (0.5 mm) for 24 h. These vials were placed in a closed glass container (20 x 30 x 25 cm), filled with moist plaster of Paris and covered with a thick layer of moist sand to maintain humid conditions close to 100% RH. This allowed animals to replenish possible water deficit to ensure that all individuals had approximately the maximal water content at the start of the measurements and an empty gut. At the start of the trait measurements, fresh weights of the animals were recorded to the nearest 0.1 μ g. Averages of the functional traits per grid cell were calculated as the average trait values of all species present.

2.3.1. Drought resistance

Interspecific differences in drought resistance were taken from Dias et al. (2013) and were based on the average survival time (time until death, in hours) of animals during exposure to drought, i.e. 85 % relative humidity. Species observed during our survey but missing in this publication (see Table 1) were measured following the same procedure, with 10 replicates per species. Isopods were individually placed in small plastic cylinders (\varnothing = 2 cm H = 3 cm) with mesh (\varnothing = 1 mm) on the bottom (Fig. S1a). These cylinders were placed on top of a plastic platform (mesh \varnothing = 1 mm) in larger plastic cylinders (\varnothing = 3.3 cm H = 11.5 cm) above a 20 ml glycerol-water solution of 42 vol%. (at 85% RH air humidity). The cylinder with isopod did not come into contact with the glycerol solution. The animals were carefully checked for signs of life every hour and time until death was recorded (to the nearest hour). Animals were considered dead if appendages did not move when the animal was carefully touched with a small soft brush. Drought survival for each species was calculated as the average time until death when exposed to drought. For individuals that died overnight, we used the median of the time of the last check in the afternoon and the first in the morning.

2.3.2. Inundation resistance

To assess interspecific differences in inundation resistance, we measured the average survival time (time until death, in hours) of animals when submerged in oxygenated water (following Moretti et al., 2017). This measure describes the capacity of an organism to withstand flooding conditions. We measured 4–20 individuals per species depending on the number of animals available. Animals were placed individually in small plastic cylinders (\varnothing = 2 cm; H = 3 cm, 9.4 cm³) with a mesh on top and bottom (0.5 mm mesh size) and submerged in a tray (31 x 21 x 9 cm) in tap water (15 °C, conductivity 51.9 mS m⁻¹). Air was bubbled through the water column to maximize the level of dissolved oxygen. Submerged animals were gently touched with a small brush to check for movement of appendages while the animal was kept under water. If antennae and legs did not move anymore the animals were recorded as dead. Small individuals (\leq 5 mm) were checked when submerged in water using a stereo microscope (magnification 4–10 times). Every animal was checked at least five times until death. For individuals that died overnight, we used the median of the time of the last check in the afternoon and the first in the morning (Fig. S1b).

2.3.3. Body size

Body size is a key characteristic of species related to many ecophysiological functional traits. Interspecific differences in body size were based on literature data. Information on body size was extracted from Vandel (1960, 1962), Dahl and Peus (1966), Gruner (1966), Hopkin (1991) and Berg and Wijnhoven (1997). For these publications it was not clear if the authors had measured body lengths themselves or if values were based on other references. Therefore, we took the maximum recorded body length (in mm) of each species (Table 1).

2.4. Statistics

All analyses were done in R v 3.3.3 (R Core Team, 2016). We calculated the community functional trait mean for each studied trait. This was done by averaging the trait values of all species present in each grid cell. Unfortunately, we did not have data on their relative abundances, so we were not able to calculate community weighted mean trait scores. However, presence or absence of species and their associated traits can be informative for understanding differences in species composition across an urbanization gradient, as the presence of a species means that the grid cell contains habitat that is within its range of habitat preferences. Four separate GLMs were used to investigate differences in the number of species, drought resistance, inundation resistance and maximum body length between grid cells, (all identity-link, normally distributed residuals). In all models, fixed factors included the level of urbanization, soil type and their two-way interaction. Terms were not removed if they were part of a higher order significant interaction. Variance distributions were tested using a Shapiro-Wilks test and the distribution residuals were evaluated by visual inspection of Quantile-Quantile plots. Generally, the assumption of parametric testing were not violated and therefore data were not transformed prior to analyses. Tukey's HSD post-hoc tests were used to test which soil types differed from each other in species number and percentage built-up area. For regressions with individual independent variables generalised least square analyses were used, with and without correction for spatial autocorrelation. Linear, exponential and polynomial regression were compared, and the best-fit equation was used. Correction for spatial autocorrelation was done following Zuur et al., 2009.

3. Results

3.1. Isopod species richness

A total of 13 terrestrial isopod species were found in the survey (Table 1), which is about 50% of the species that can be found in the lowlands of Europe. Between 1 and 12 species were found per grid cell (on average 6.4 species \pm 0.10 SEM, Fig. 2). Five generalist species were found in almost all grid cells (78–100% of the grid cells), i.e. *Porcellio scaber*, *Oniscus asellus*, *Philoscia muscorum*, *Trichoniscus pusillus* s.l. and *Armadillidium vulgare* (Table 1, Fig. S2). Grid cells with more than five species always contained these generalist species, while grid cells with fewer species contained usually a subset of these generalists. Detailed distribution maps of all species are given in the supplementary materials (Fig. S2).

Grid cells with clay soil contained on average a larger number of species than grid cells with peat soil (7.2 \pm 2.1 and 5.6 \pm 1.5 species, respectively) and the average number of species in the grid cells with a mixture of both soils was intermediate, i.e. clay with peat and peat with clay (6.8 \pm 1.9 and 6.3 \pm 1.9 species, respectively) (Fig. 3: ANOVA, $F_{3,348} = 13.91$, $p < 0.001$). Also, the maximum number of species was higher in clay soil (12 species) compared to peat soil (10 species). The frequency distributions of the number of species per grid cell in the four soil type categories were similar and did not differ from the total dataset (Fig. S3).

Percentage built-up area, as a measure of urbanisation, had a significant overall effect on species richness (GLM, $F_{1,350} = 9.83$, $p = 0.002$). There was a significant interaction between soil type and proportion built-up area on species number (Table 2, Fig. 4; GLM, $F_{3,347} = 6.85$, $p = 0.002$). For clay and peat with clay soils, proportion built-up area had a negative effect on species number (GLS, $t_{74} = -3.256$, $p = 0.002$; $t_{93} = -2.006$, $p = 0.048$). Species richness declined from 8 species in grid cells without buildings to 6 species in fully built-up areas. For peat soils we found the highest species numbers at intermediate levels of urbanization (GLS, $t_{121} = -3.706$, $p < 0.001$). For clay with peat grid cells, we observed no effect of urbanisation on species number. At low

	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	
493	6	6	8	6	9	9	8	6	6	8	7	6	4	8	4	9	5	5	6	3	4	4	4	3	493
492	5	7	5	2	5	6	5	3	6	9	6	6	5	4	6	7	4	4	4	4	2	5	4	3	492
491	6	7	5		4	6	6			4	5	3	6	5	5	6	5	4	4	5	5	6	4	3	491
490	7	8			6	6	5	6	6	4	6	6	5	6	6	6	4	3		4	3				490
489	6	7	7	7	5	6	6	6	5	6	7	7	5	10	8	6	5	3	8	5	8				489
488	8	5	8	6	5	5	7	6	6	5	6	7	9	8	8	7	5	4	9	10	5				488
487	10	6	6	8	6	4	5	5	7	3	3	4	6	7	8	5	5	7	9	9					487
486		6		10	5	5	6	5	7	4	5		7	5	7	10	7								486
485		7	11	3	5	4	4	6	5	6	5	4	5	7	8	10	8	12							485
484	9	12	5	7	7	5	8	5	7	3	4		4	11	5	12	7	6	9	7	6				484
483	11	12	10	7	5	6	7	6	5	7		6	10	6	5	6		7	9	10	11	10	9	3	483
482	10	9	9		8	6	5	6	10	10	6	10	7	6	7	5	9	6	6	9	7	10	4	5	482
481	9	8	8			5	12	7	6	6	6	9	10	6	6	6	6	6	8	9	6		7		481
480	8					6	10	6	5	4	6	7	6	4	6	6	6	6	8	9	5	6	6	4	480
479					7	7	6	6	5	5		8	10	8	5	5		6	4	9	9	4	4		479
478		6	5	6	8	7	7	6	8	8		7	6		5	5		3	4	7	3		5	2	478
477	6	7	7	7	5	4	6	7	9	5	8		5	5	5	7	5		6	9			8	2	477
476	5	6	5	4			7	6	5	5	11			5	7	7		5	7	5	8	7	7	7	476
	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	

Fig. 2. Number of isopod species per 1 km² grid cell within and around the city of Amsterdam. Colours of the cells represent species numbers: green: >7 species; yellow: 5–7 species; red: <5 species; white: insufficient data; blue stripes: lake IJsselmeer. Numbers on the outside of the table indicate coordinates of the Dutch grid system. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

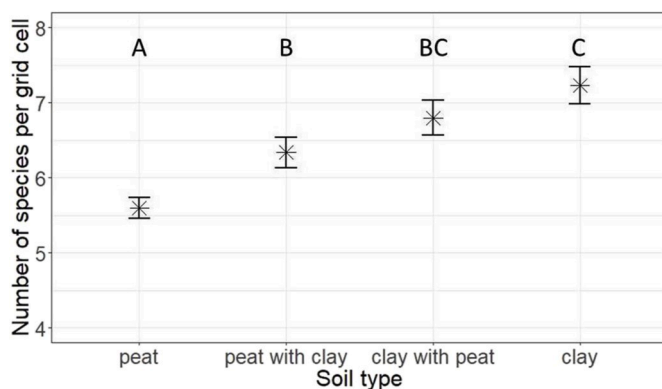


Fig. 3. Average number (\pm SEM) of isopod species per soil type (peat >90% peat; peat with clay = 50–90% peat; clay with peat = 50–90% clay; and clay >90% clay). Capital letters that do not overlap between soil types indicate a significant difference ($P < 0.05$) in Tukey's HSD post hoc test.

level of urbanisation, a positive effect on species number was observed for peat soils. Species richness increased from 4 to 6 species when urbanisation increased from 0–50% built-up area. However, at higher levels of urbanisation a negative effect on species number was seen and decreased species number from 6 to 5 species (peat soils) after an increase in built-up area from 50% to 100%.

3.2. Functional traits

For some species, values for drought resistance and inundation resistance were not available from the literature and were measured. Average trait values per species are summarized in Table 1.

Average drought resistance of the isopod species was significantly higher with increasing levels of urbanisation across soil types (Table 1; GLM, $F_{1,350} = 20.09$, $p < 0.001$). There was a significant difference between soil types (GLM, $F_{3,350} = 4.81$, $p = 0.003$), but the interaction between soil type and percentage built-up area was not significant (GLM, $F_{3,347} = 0.09$, $p = 0.96$) (Tables 3 and 4, Fig. 4b).

For inundation resistance we found a significant interaction between soil type and percentage built-up area (GLM, $F_{3,347} = 3.88$, $p = 0.009$). A post-hoc test showed that inundation resistance was lower with increasing level of urbanisation for clay soils (GLS, $t_{72} = -1.825$, 0.072) and for peat soils we found the highest inundation resistance at intermediate levels of urbanization (GLS, $t_{121} = -2.254$, $p = 0.026$). We found no effect of urbanisation on inundation resistance for the other two soil types. The average inundation resistance of isopod communities on clay soils decreased from 125 to 80 h of survival when urbanisation increased from 0% to 100%. Inundation resistance increased from 75 to 90 h when urbanisation increased from 0–50% built-up area and decreased species from 90 to 75 h after an increase in built-up area from 50% to 100%. (Tables 2 and 3, Fig. 4c).

Maximum body length was significantly higher with increasing levels of urbanisation (Table 2, Fig. 4d; GLM, $F_{1,351} = 20.09$, $p < 0.001$) and differed between soil types (GLM, $F_{3,350} = 4.66$, $p = 0.003$), but there was no significant interaction between both factors. The average

Table 2

Summary output from the generalised linear models of the effect of soil type and proportion built-up area on species richness and the four response traits. P values < 0.05 are in bold script.

Fixed factor	Species number			Drought resistance			Inundation resistance			Maximum body length		
	F	df	p	F	df	p	F	df	p	F	df	p
Soil type	6.85	3, 347	0.002	4.81	3, 350	0.003				4.66	3, 350	0.003
% built-up area				20.09	1, 350	< 0.001				20.09	1, 351	< 0.001
Soil type x % built-up area				0.09	3, 347	0.965	3.88	3, 347	0.009	1.22	3, 347	0.3

maximum body length increased from 11 to 13 mm when urbanisation increased from 0% to 100%. Post-hoc testing showed that this effect was significant for peat soils, peat with clay and clay soils (GLS resp., $t_{121} = 1.992$, $p = 0.049$; $t_{93} = 2.499$, $p = 0.014$ and $t_{74} = 2.183$, $p = 0.032$). No effect was found for clay with peat soils (Tables 3 and 4, Fig. 4d).

The effect of rural versus urban green was very small compared to the effect of built-up area. This was at least partly explained (Table 4) by the fact that the differences between soil types in percentage rural green of total area or percentage urban green of total area were very small within the 0–50% built-up class and 50–100% built-up class, respectively. Therefore, there was no need to do further in-depth analyses of the effect of rural versus urban green on isopod species richness.

4. Discussion

We found support for our prediction that the response of terrestrial isopod species richness across an urbanisation gradient depends on soil type. Indeed urbanisation had a negative effect on isopod species richness only in clay soils, whereas in peat soils we found a hump-back shape relationship. In contrast, functional traits showed a consistent relationship with urbanisation. We expected that enhanced levels of urbanisation would be associated with increased habitat temperature and decreased water infiltration, leading to drier soils for all soil types, and consequently, increasingly drought resistant communities. We indeed found a positive effect of urbanisation on community average drought resistance and maximum body length for all soil types and a negative effect on average inundation resistance for communities on clay soils. The current study is, to our knowledge, the first to focus on context-dependency of the impact of urbanisation on taxonomic diversity, and the first to demonstrate that a focus on functional traits directly related to stress imposed by urbanisation can reduce this context-dependency.

4.1. Species richness response to urbanization

Like most studies on the impact of urbanisation on biodiversity (McKinney, 2002; Seto et al., 2012), we found an overall negative effect on species richness at high levels of urbanisation, but at moderate levels of urbanisation the effect on isopod species richness was soil type dependent. An increase in urbanisation negatively affected species richness in clay soils, showed a hump-back shape relationship in peat soils and no effect in mixed soils. We hypothesize that two different mechanisms operating simultaneously might explain the observed pattern. A relatively low level of urbanisation may promote environmental heterogeneity, while pockets of more natural, often threatened vegetation are preserved, for example in old parks (Aronson et al., 2014). Therefore, many studies find a peak of species richness in suburbs (McKinney, 2008), at moderate levels of urbanisation, which is often explained by the intermediate disturbance hypothesis (Connell, 1978). We found a positive effect of urbanization on species richness for peat soils only, because this soil type has a rather low species richness. A second possible mechanism for the soil type dependent effect could be the improvement of soil quality in urban environments, particularly Ca content. Compared to clay soil, peat has a low pH resulting from high organic acid and low base cation content, including low Ca content (Bolt and Bruggenwert, 1978). For natural peat soils, addition of high quality pot soil (i.e. a high Ca availability) in parks and gardens increases

species richness. Pot soil addition to natural (Ca-rich) clay soils, to improve soil structure, will decrease Ca content, which may reduce species richness. So, from low to moderate levels of urbanisation the effect of changes in soil chemistry due to soil improvement on isopod species richness depends on the original rural soil chemical quality and might explain the observed context-dependency.

However, when the level of urbanisation further increases (i.e. with built-up area more than 50%) habitat fragmentation and urban heating (i.e. resulting in soil drought) may become more important than small changes in the chemical quality of soils. At high proportions of built-up area less habitat is available, patch size decreases, and subsequently patch isolation increases. This may result in smaller populations, and communities may be more vulnerable to species losses due to increasing temperature and decreasing soil moisture with a higher chance of local extinction under extreme climatic events, coupled to lower recolonization from the meta-community (Åström and Bengtsson, 2011).

4.2. Functional trait responses to urbanisation

In accordance with our expectation, we found that, on average, community drought resistance increased with an increase in the percentage of built-up area, across all soil types. This suggests that drought resistance is a good predictor of how isopod community composition will cope with urbanisation, even though differences in drought resistance between soil types were very small (range 26.7–30.8 h). We feel that the patterns for drought resistance and body length against urbanisation level, although of rather low r^2 , are ecologically relevant, also because these relations are generally similar and positive across the different soil types. For inundation resistance, however, relationships with urbanisation level were mostly flat while soil types different substantially in inundation resistance (range 83.3–104.9 h). Body length generally had positive relationships with urbanisation but with low explanatory power, while the differences between soil types were small (range 11.9–12.8 mm) but probably ecologically relevant. Soil moisture is one of the most important factors that determine the composition of isopod communities (Hornung, 2011), and for natural soils it was shown that the trait drought tolerance is a good predictor of how changes in soil moisture effect isopod community composition (Dias et al., 2013). An increase in community drought resistance for peat soil with increasing urbanisation is the result of drought resistant species that enter the communities, such as *Trachelipus rathkii* and *Porcellio spinicornis*. For clay soils, on the contrary, an increase in community drought resistance is explained by the loss of drought-sensitive species, such as *Ligidium hypnorum* and *Trichoniscoides albidus*. As drought resistance is negatively correlated with inundation resistance (Fig. S5), we observed a negative effect of percentage built-up area on average inundation resistance. Hence, the context-dependent shift in community composition can be understood from ecophysiological traits of component species.

Other studies have also reported effects of urbanisation on functional trait composition. For example, beetle species in cities have a higher thermal preference and higher dispersal ability than species in rural areas (Piano et al., 2017), body mass of millipede communities decreases with increasing level of urbanisation (Bogyó et al., 2015) and wing length of butterfly communities increases with increasing land-use intensity (Börschig et al., 2013). Shifts of functional diversity in terms of species traits were also found in studies that did not show any effect on

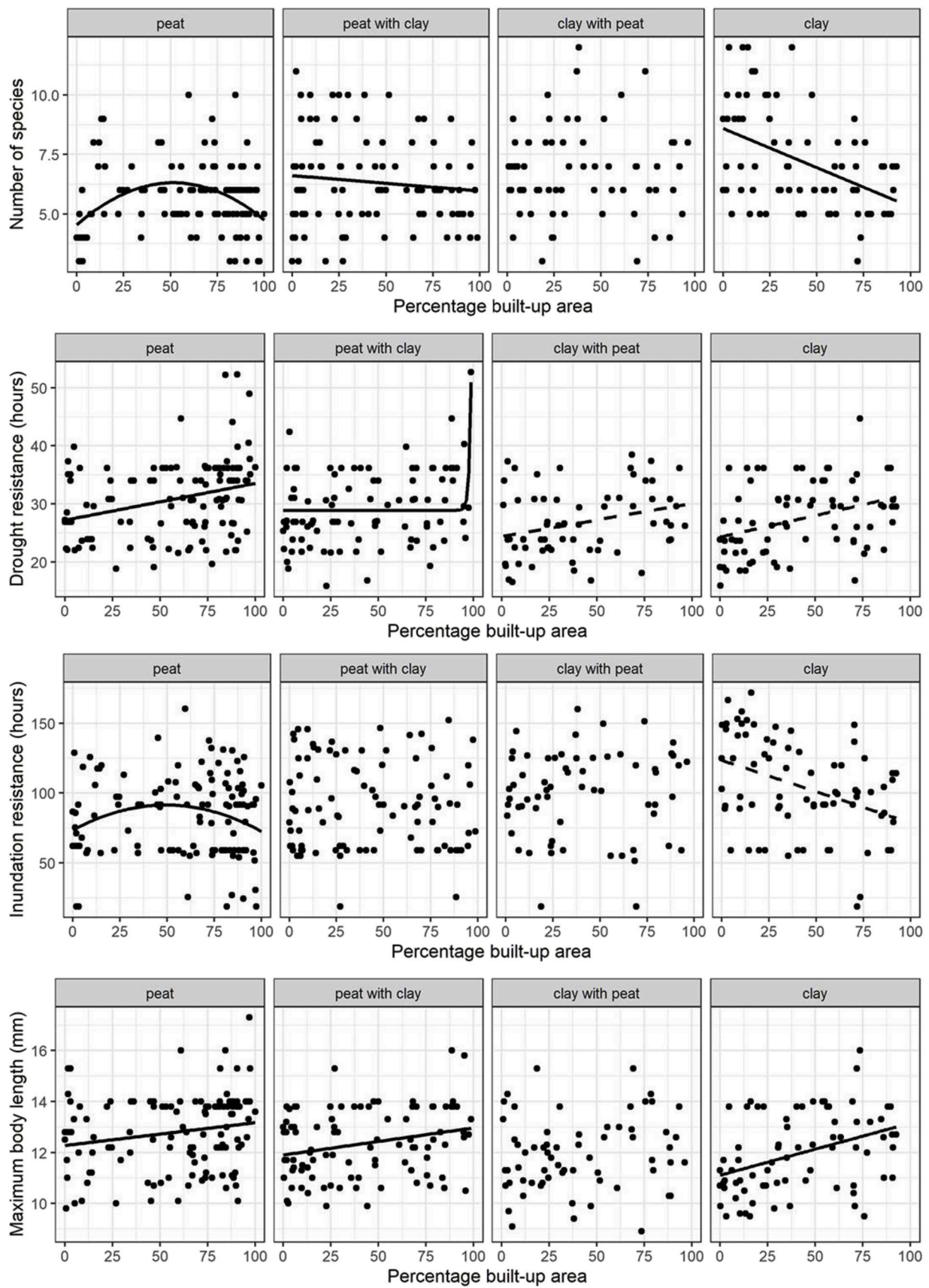


Fig. 4. Effect of the level of urbanisation (percentage of built-up area in each grid cell) on Number of species (A) and community functional trait means: Drought resistance (B); Inundation resistance (C) and Maximum body length (D) per grid cell, for four soil type classes (peat >90% peat; peat with clay = 50–90% peat; clay with peat = 50–90% clay; and clay >90% clay). Trendlines are shown for significant relations. Note that the trend lines do not extend beyond the data range. The highest value for urbanisation level was 99.5%, which meant 0.5% (0.5 ha) was unbuilt, providing enough space to contain more than 1–2 species.

Table 3

Summary output from generalised least square analyses of the effect of proportion built-up area per soil type on species richness and the four response traits. Results of the analyses without correction for spatial autocorrelation are given between brackets. Degrees of freedom are similar for the analyses with and without correction. Linear, exponential and polynomial regression were compared, and the best-fit equation was used. P values < 0.05 are in bold script.

	Soil type	t	df	P	Correction	equation
Species number	Peat	−3.706 (−4.095)	121	<0.001 (<0.001)	corExp	poly
	Peat with clay	−2.006 (−1.042)	93	0.048 (0.300)	corExp	lineair
	Clay with peat	−0.464 (0.035)	64	0.644 (0.972)	corExp	lineair
	Clay	−3.256 (−4.333)	74	0.002 (<0.001)	corExp	lineair
	Peat	3.220 (3.586)	121	0.002 (<0.001)	corRatio	lineair
Drought resistance	Peat with clay	3.732 (3.814)	93	<0.001 (<0.001)	corRatio	exp.
	Clay with peat	1.977 (2.380)	64	0.053 (0.020)	corRatio	lineair
	Clay	1.640 (3.176)	74	0.106 (0.002)	corRatio	lineair
	Peat	−2.254 (−2.178)	121	0.026 (0.031)	corRatio	poly
	Peat with clay	−1.181 (−0.711)	93	0.241 (0.479)	corRatio	lineair
Inundation resistance	Clay with peat	0.440 (0.440)	64	0.662 (0.662)	corRatio	lineair
	Clay	−1.825 (−3.546)	74	0.072 (<0.001)	corRatio	lineair
	Peat	1.992 (2.197)	121	0.049 (0.003)	corRatio	lineair
	Peat with clay	2.499 (2.499)	93	0.014 (0.014)	corRatio	lineair
	Clay with peat	1.108 (1.109)	64	0.272 (0.272)	corRatio	lineair
Maximum body length	Clay	2.183 (3.569)	74	0.032 (<0.001)	corRatio	lineair

local taxonomic biodiversity (Hornung et al., 2007, Baiser and Lockwood, 2011). Together with our results, this evidences that functional traits give a better and mechanistic insight in the response of animal communities to environmental stress than taxonomic diversity does.

We found an effect of urbanisation on functional trait composition

based on presence and absence but we expect stronger relationships if the community-weighted mean trait values could be calculated. The rationale is that the trait of the most dominant species gives a better reflection of the relationship between environmental condition and community functioning than the trait value of a rare species (“mass ratio hypothesis”: Grime, 1998). As we had access to presence/absence data only, all our species contributed equally to the community trait average. Although we did observe a consistent trait response to urbanisation, Dias et al. (2013) showed that simple mean trait values do not necessarily predict the effect of shifts in soil moisture on isopod community trait composition (in terms of body size and drought tolerance), while weighting the trait values of species by their relative abundance gave a clear signal. More research is needed that includes relative abundance of species to better understand the relationship between environmental change, species abundances, traits and biodiversity. Moreover, the actual size and isolation of habitat patches that have been surveyed in a grid cell could contribute to the large variance in the relationship between percentage built-up area and species number. Habitat size and isolation might impact immigration and emigration dynamics, as small islands within a 50% urbanisation grid cell might contain a lower number of isopod species than a single large island. Therefore, we suggest to include information on patch size and distances in future research on the relationship between urbanisation and species richness.

5. Conclusion

In this study, we showed that the effect of urbanisation on isopod taxonomic and functional diversity was modified by pure peat and pure clay soil. As the composition of many groups of soil fauna are strongly dependent on soil type, we expect that other soil animal taxa will show similar responses to urbanisation. We conclude that interaction with classical urbanisation drivers, i.e. climate and habitat loss, other factors, specifically soil type, introduces an important, but often overlooked context-dependency to understand the effects of urbanisation on taxonomic and functional diversity of isopods. We also showed that urbanisation had an effect on isopod functional trait composition and we expect to find similar effects on other soil taxa. Whether the latter would also be dependent on soil type, not only for isopods but also for other detritivores, or herbivores, should be high on the research agenda given their important role in key soil processes.

We hypothesize that shifts in isopod community composition will also lead to changes in biogeochemical cycling with urbanisation through shifts in isopod food consumption. Like drought- and inundation resistance, litter consumption rate is also correlated with isopod body size (Reichle, 1968; Vilisics et al., 2012). Consequently, environmental filtering based on species drought and inundation resistances are expected to also lead to shifts in community average litter consumption rates. Therefore, we expect that urbanisation has a positive effect on average litter consumption rate by isopods, as an indirect consequence

Table 4

Summary of relative land-use (% coverage by urban habitat or rural habitat) on different soil types in and around the city of Amsterdam, and the associated mean number of isopod species per km² grid cell. For each soil type the top line gives the overall values and the middle and bottom lines the values per class in terms of % built-up.

	Class of % built up-area	% built-up area	% urban green of total green area	% urban green of total area	% rural green of total area	Number of species
Peat	0–100%	57.5	59.2	15.2	27.3	5.6
	0–50%	17.8	19.5	13.8	68.5	5.5
	50–100%	78.6	80.2	15.9	5.5	5.7
Peat with Clay	0–100%	43.2	39.2	12.5	44.4	6.4
	0–50%	20.0	17.9	11.8	68.2	6.5
	50–100%	78.6	72.5	13.9	7.5	6.1
Clay with peat	0–100%	40.5	43.1	17.7	41.8	6.8
	0–50%	19.9	24.4	18.3	61.8	6.9
	50–100%	74.9	74.4	16.7	8.4	6.6
Clay	0–100%	41.4	27.9	11.6	47.0	7.2
	0–50%	20.8	15.8	11.2	67.9	8.0
	50–100%	73.3	46.7	12.1	14.6	6.1

of an increase in species' average drought resistance and a decrease in species' average inundation resistance.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2020.107851>.

References

- Aronson, M.F., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Winter, M., 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281 (1780), 20133330.
- Aronson, M.F., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P.S., Cilliers, S.S., Goddard, M.A., Hahs, A.K., Herzog, C., Katti, M., La Sorte, F.A., Williams, N.S.G., Zipperer, W., 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97 (11), 2952–2963.
- Åström, J., Bengtsson, J., 2011. Patch size matters more than dispersal distance in a mainland-island metacommunity. *Oecologia* 167 (3), 747.
- Baier, B., Lockwood, J.L., 2011. The relationship between functional and taxonomic homogenization. *Global Ecology and Biogeography* 20 (1), 134–144.
- Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515 (7528), 505.
- Berg, M.P., Soesbergen, M., 1998. In: Melchers, M., Soesbergen, M., Timmermans, G. (Eds.), *Paardenbijten en mensentreters, de veelpoters van Amsterdam*. Schuyt Co, Haarlem, pp. 129–147.
- Berg, M.P., Soesbergen, M., Tempelman, D., Wijnhoven, H., 2008. Verspreidingsatlas Nederlandse landpissebedden, duizendpoten en miljoenpoten. European Invertebrate Survey, Leiden (Vrije Universiteit Amsterdam).
- Berg, M.P., Wijnhoven, H., 1997. Naamlijst van de Nederlandse landpissebedden (Crustacea: isopoda: oniscidea). *Nederlandse Faunistische Mededelingen* 7 (6), 31–34.
- Bardgett, R., 2005. *The Biology of Soil: a Community and Ecosystem Approach*. Oxford University Press.
- Bíla, K., Moretti, M., de Bello, F., Dias, A.T., Pezzatti, G.B., Van Oosten, A.R., Berg, M.P., 2014. Disentangling community functional components in a litter-macrodetritivore model system reveals the predominance of the mass ratio hypothesis. *Ecology and Evolution* 4 (4), 408–416.
- Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. *Oecologia* 165 (3), 553–565.
- Bogoy, D., Magura, T., Simon, E., Tóthmérész, B., 2015. Millipede (Diplopoda) assemblages alter drastically by urbanisation. *Landscape and Urban Planning* 133, 118–126.
- Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology* 18 (3), 1152–1162.
- Bolt, G.H., Bruggenwert, M.G.M., 1978. *Soil Chemistry. A. Basic Elements*. Elsevier Scientific Publishing Company.
- Börschig, C., Klein, A.M., von Wehrden, H., Krauss, J., 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology* 14 (7), 547–554.
- Caruso, T., Migliorini, M., Rota, E., Bargagli, R., 2017. Highly diverse urban soil communities: does stochasticity play a major role? *Applied Soil Ecology* 110, 73–78.
- CBS, 1996. *Bestand Bodemgebruik 1996*. Centraal Bureau voor de Statistiek Den Haag/Heerlen.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199 (4335), 1302–10.
- Dahl, M., Peus, F., 1966. *Die Tierwelt Deutschlands*, T 51. VEB Gustav Fischer, Jena, pp. 39–44.
- Dale, A.G., Frank, S.D., 2014. Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications* 24 (7), 1596–1607.
- David, J.F., 2014. The role of litter-feeding macroarthropods in decomposition processes: a reappraisal of common views. *Soil Biology and Biochemistry* 76, 109–118.
- De Gans, W., 2006. *ANWB Geologieboek Nederland*. ANWB Media-Boeken Gidsen.
- Dias, A.T., Krab, E.J., Mariën, J., Zimmer, M., Cornelissen, J.H., Ellers, J., Wardle, D.A., Berg, M.P., 2013. Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia* 172 (3), 667–677.
- Díaz, S., Purvis, A., Cornelissen, J.H., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., Pearse, W.D., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* 3 (9), 2958–2975.
- Filser, J., Faber, J.H., Tiunov, A.V., Brussaard, L., Frouz, J., De Deyn, G., Uvarov, A.U., Berg, M.P., Lavelle, P., Loreau, M., Wall, D.H., Querner, P., Eijsackers, H., Jiménez, J.J., 2016. Soil fauna: key to new carbon models. *Soils* 2 (4), 565–582.
- Fournier, B., Gillet, F., Le Bayon, R.C., Mitchell, E.A., Moretti, M., 2015. Functional responses of multitaxa communities to disturbance and stress gradients in a restored floodplain. *Journal of Applied Ecology* 52 (5), 1364–1373.
- Fussey, G.D., 1984. The distribution of the two forms of the woodlouse *Trichoniscus pusillus* Brandt (Isopoda: oniscoidea) in the British Isles: a reassessment of geographic parthenogenesis. *Biological Journal of the Linnean Society* 22 (4), 309–321.
- Goddard, M.A., Dougill, A.J., Benton, T.G., 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution* 25 (2), 90–98.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86 (6), 902–910.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319, 756–760.
- Gruner, H.-E., 1966. *Krebstiere oder Crustacea V. Isopoda*. Tierwelt Deutschlands 53, 1–230.
- Harding, P.T., Sutton, S.L., 1985. *Woodlice in Britain and Ireland: Distribution and Habitat*. Institute of Terrestrial Ecology.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review Ecology and Systematics* 36, 191–218.
- Heemsbergen, D.A., Berg, M.P., Loreau, M., Van Hal, J.R., Faber, J.H., Verhoef, H.A., 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306 (5698), 1019–1020.
- Hillel, D., 2013. *Fundamentals of Soil Physics*. Academic press.
- Hopkin, S.P., 1991. *A Key to the [37 Species of] Woodlice of Britain and Ireland*. Field Studies (United Kingdom).
- Hornung, E., Tóthmérész, B., Magura, T., Vilisics, F., 2007. Changes of isopod assemblages along an urban-suburban-rural gradient in Hungary. *European Journal of Soil Biology* 43 (3), 158–165.
- Hornung, E., 2011. Evolutionary adaptation of oniscidean isopods to terrestrial life: structure, physiology and behavior. *Terrestrial Arthropod Reviews* 4 (2), 95–130.
- Jacobson, C.R., 2011. Identification and quantification of the hydrological impacts of imperviousness in urban catchments: a review. *Journal of Environmental Management* 92 (6), 1438–1448.
- Jesse, W.A., Behm, J.E., Helmus, M.R., Ellers, J., 2018. Human land use promotes the abundance and diversity of exotic species on Caribbean islands. *Global Change Biology* 24 (10), 4784–4796.
- Jiang, Y., Fu, P., Weng, Q., 2015. Assessing the impacts of urbanization-associated land use/cover change on land surface temperature and surface moisture: a case study in the midwestern United States. *Remote Sensing* 7 (4), 4880–4898.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P.O.W.H., Heal, O.W., Dhillon, S., 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology* 33 (4), 159–193.
- Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Diaz, S., Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science* 24 (5), 942–948.
- Lavelle, P., Spain, A.V., 2001. *Soil Ecology*. Springer Science Business Media.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52 (10), 883–890.
- McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11 (2), 161–176.
- Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcarate, F.M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. Paulo, Ellers, J., Berg, M.P., 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology* 31 (3), 558–567.
- Morón-Ríos, A., Rodríguez, M.Á., Pérez-Camacho, L., Rebollo, S., 2010. Effects of seasonal grazing and precipitation regime on the soil macroinvertebrates of a Mediterranean old-field. *European Journal of Soil Biology* 46 (2), 91–96.
- Oke, T.R., Johnson, G.T., Steyn, D.G., Watson, I.D., 1991. Simulation of surface urban heat islands under 'ideal' conditions at night Part 2: diagnosis of causation. *Boundary-Layer Meteorology* 56 (4), 339–358.
- Piano, E., Souffreau, C., Merckx, T., Baardens, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J.M.T., Fontaneto, D., Gianuca, A.T., Govaert, L., Hanashiro, F.T.T., Higiuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Pinseel, E., Sablon, R., Schön, I., Stoks, R., Van Doninck, K., Van Dyck, H., Vanormelingen, P., Van Wichelen, J., Vyverman, W., De Meester, L., Hendrickx, F., 2017. Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology* 23 (7), 2554–2564.
- Pickett, S.T., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E., Kaushal, S.S., Marshall, V., McGrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy, A., Warren, P., 2011. Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management* 92 (3), 331–362.
- Pavao-Zuckerman, M.A., Coleman, D.C., 2007. Urbanization alters the functional composition, but not taxonomic diversity, of the soil nematode community. *Applied Soil Ecology* 35 (2), 329–339.
- Pouyat, R.V., Szlavecz, K., Yesilonis, I.D., Groffman, P.M., Schwarz, K., 2010. Chemical, physical, and biological characteristics of urban soils. *Urban ecosystem ecology* 55, 119–152.
- Ramirez, K.S., Leff, J.W., Barberán, A., Bates, S.T., Betley, J., Crowther, T.W., Kelly, E.F., Oldfield, E.E., Shaw, E.A., Steenbock, C., Bradford, M.A., Wall, D.H., Fierer, N., 2014. Biogeographic patterns in below-ground diversity in New York City's Central Park are similar to those observed globally. *Proceedings of the Royal Society of London B Biological Sciences* 281 (1795), 20141988.

- R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Reichle, D., 1968. Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. *Ecology* 49 (3), 538–542.
- Roth, M., Oke, T.R., Emery, W.J., 1989. Satellite-derived urban heat islands from three coastal cities and the utilization of such data in urban climatology. *International Journal of Remote Sensing* 10 (11), 1699–1720.
- Schmalfuss, H., 2003. World catalog of terrestrial isopods (Isopoda: oniscidea). *Stuttgarter Beiträge zur Naturkunde, Series A*, Nr 654, 341.
- Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences* 109 (40), 16083–16088.
- Vandel, A., 1960. Isopodes terrestres. Part 1 Faune de France 64. Lechevalier, Paris.
- Vandel, A., 1962. Isopodes terrestres. Part 2 Faune de France 66. Lechevalier, Paris.
- Vilisics, F., Elek, Z., Lövei, G.L., Hornung, E., 2007. Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark. *Pedobiologia* 51 (1), 45–53.
- Vilisics, F., Hornung, E., 2009. Urban areas as hot-spots for introduced and shelters for native isopod species. *Urban Ecosystems* 12 (3), 333–345.
- Vilisics, F., Szekeres, S., Hornung, E., 2012. Size dependent differences in litter consumption of isopods: preliminary results. *ZooKeys* 176, 247.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116 (5), 882–892.
- Yang, J.L., Zhang, G.L., 2015. Formation, characteristics and eco-environmental implications of urban soils—A review. *Soil Science & Plant Nutrition* 61 (Suppl. 1), 30–46.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A., Smith, G.M., 2009. Mixed effect models and extensions in ecology with R. <https://doi.org/10.1007/978-0-387-87458-6>.